Palaeoplethodon hispaniolae gen. n., sp. n. (Amphibia: Caudata), a fossil salamander from the Caribbean

George Poinar Jr. & David B. Wake

Abstract

A salamander hatchling, *Palaeoplethodon hispaniolae* gen. n., sp. n. (Amphibia: Caudata), is described from Dominican Republic amber. While physical features align the fossil with members of the family Plethodontidae, the short forelimb with the foot lacking distinct digits and the long hind limb with elongated foot and strongly fused digits, as well as its presence in 15–40 mya Dominican amber, distinguish the fossil from previously described salamanders. The apparent 13–14 costal grooves and strongly webbed digits are characters shared with members of the extant plethodontid genus *Bolitoglossa* Peters, 1879, the most speciose genus of Neotropical salamanders. This is the first salamander recovered from any amber source and the first undisputed salamander reported from the Caribbean region.

K e y w o r d s : Salamander, fossil, *Palaeoplethodon hispaniolae*, Caudata, Plethodontidae, Dominican amber.

1. Introduction

Over the years, remains of frogs, lizards, birds and mammals have been found in various amber deposits around the world, but no salamanders have ever been reported (Poinar 1992; Poinar & Poinar 1999). The present study describes a salamander in Dominican Republic amber that is assigned to the family Plethodontidae, a widespread family of salamanders that has colonized the Neotropical region. Plethodontids are characterized by the absence of lungs, the presence of a nasolabial groove in metamorphosed individuals, osteological novelties and limbs with fours toes on the fore feet and five on the hind feet (Wake 1966). The tropical representatives of the family deposit their eggs on land and the larval stage develops within the egg and emerges as a juvenile hatchling that is essentially a miniature version of the adult. The fossil salamander described below is considered to be a hatchling and the strongly webbed digits and long tail suggest it was an arboreal species.

A c k n o w l e d g m e n t s

The authors thank Brian L. Sidlauskas, Department of Fisheries and wildlife, Oregon State University, for taking the X-ray photo in Fig. 11 and Sean Rovito for taking the photo of the extant *Bolitoglossa chinanteca* in Fig. 14. We also thank Susanne Stieger-Vanegas of the College of Veterinary Medicine and Urszula Iwaniec, College of Public Health and Human Sciences at Oregon State University for taking additional X-rays of the fossil and Robert T. Mason of the Department of Zoology, Oregon State University for support and assistance. Grateful appreciation is extended to the referees, whose comments enhanced the manuscript.

2. Materials and methods

The salamander fossil originated from an amber mine in the northern mountain range (Cordillera Septentrional) of the Dominican Republic between Puerto Plata and Santiago. Amber obtained from these mines was produced by *Hymenaea protera* Poinar (1991) (Fabaceae). Dating of Dominican amber is uncertain with the youngest proposed ages of 20–15 mya based on foraminifera (Iturralde-Vincent & MacPhee 1996) and the oldest ages of 45–30 mya based on coccoliths (Cepek in Schlee 1990). These dates are based on microfossils recovered from the strata containing the amber, which had been re-deposited in Upper Eocene to Lower Miocene turbiditic sandstones of the Mamey Group (Draper et al. 1994). Dilcher et al. (1992) felt that because the amber had already matured by the time it was re-deposited into the marine basins, it could as old as Late Eocene. The discovery of Early Oligocene amber in Puerto Rico and Maastrichtian-Paleocene amber in Jamaica (Iturralde-Vinent 2001) shows that amber deposits from different ages occur throughout the Greater Antilles.

The piece of amber containing the fossil is hemispheric in shape, measuring 20 mm in length, 8 mm in greatest width and 8 mm in depth. Observations and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 600 X. Helicon Focus Pro X64 was used to stack photos for better clarity and depth of field. Radiographs were taken on a Faxitron MX-20 Digital Radiography System set at 20 kV and 0.3 mA with an exposure of 160 seconds.

3. Description

Class Amphibia Latreille, 1806

Order Caudata Scopoli, 1777

Family Plethodontidae Gray, 1850

Genus *Palaeoplethodon* nov.

Diagnosis: Same as type species since monotypic.

Type species: *Palaeoplethodon hispaniolae* gen. n., sp. n.

Palaeoplethodon hispaniolae gen. n., sp. n.
Figs. 1-13

Etymology: The generic name is from the Greek "Paleo" = old and "Plethodontidae", the family of salamanders to which the fossil belongs. The specific epithet refers to the locality of the specimen.

Type: Holotype (accession # AM-3-15) deposited in the Poinar amber collection maintained at Oregon State University.

Type locality: Amber mine in the northern mountain range (Cordillera Septentrional) of the Dominican Republic.

Diagnosis: Characters of the fossil place it among the extant tropical genera of Plethodontidae (Wake & Elias 1983). The long hind limbs (almost twice the length of the forelimbs), completely rounded fore foot (manus) and elongate hind foot (pes) with tightly webbed digits separates the new species from previously known salamanders.

Description: Body diminutive, somewhat stocky; head relatively wide with blunt, short snout (Figs. 1-5); eyes moderately large (Fig. 3); nostrils slightly protruding, nasolabial grooves faint; teeth not visible; forelimb less than half (0.41) length of hind limb, manus pad-like, with digits completely fused (Figs. 6, 7); hind limbs outstretched (Fig. 8), hind pes longer than wide, bearing five syndactylous digits with digits one and two almost completely fused (Fig. 9); trunk with faint costal grooves (Fig. 10); tail not strongly compressed laterally, with a weak basal constriction. Total length (body and tail), 18 mm; body length (snout to vent), 9 mm; head length, 1.4 mm; head width, 1.3 mm; head depth, 0.8 mm; eye diameter, 0.38 mm; length snout to forelimb, 1.8 mm; length axilla to groin, 4.0 mm; length tail, 9.0 mm; tail width at base, 1.2 mm; length forelimb, 1.6 mm; length hind limb, 2.9 mm.

Remarks: The specimen is complete except for the left forelimb, which has been severed from the body with only some basal tissue and a portion of the humerus remaining, and the tip of the right hind limb that was accidently removed during preparation of the specimen. The basal portion of the remaining right forelimb is bent back under the body. The integument is wrinkled and reticulated and the eyes are collapsed against the head, a result of the desiccation process that occurs during the fossilization of amber specimens. Some plant debris is scattered throughout the amber piece and some small pieces of inorganic material are adjacent to the tail. The color of the specimen is dark brown, but since the fossilization process is often accom-

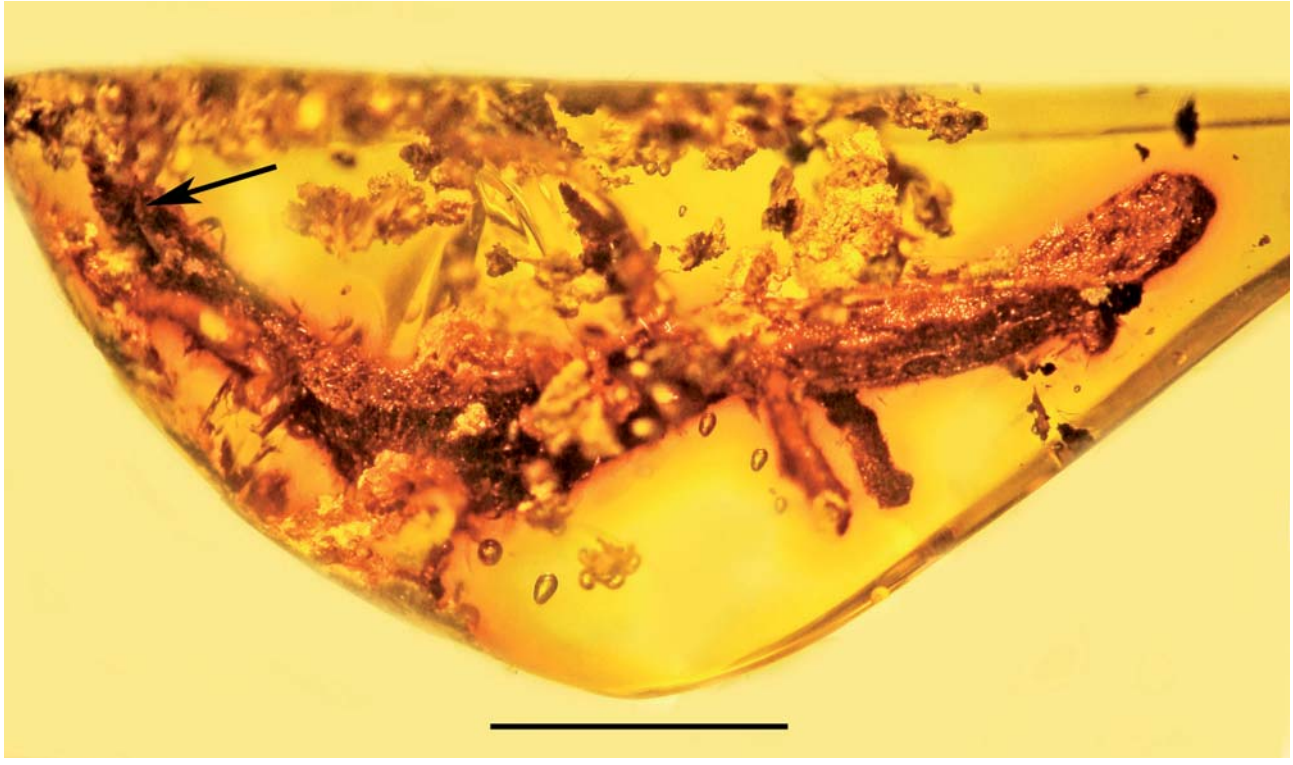


Fig. 1. Lateral view of complete specimen of *Palaeoplethodon hispaniolae* gen. n., sp. n. in Dominican amber. Arrow shows tip of tail. Bar = 4.3 mm.

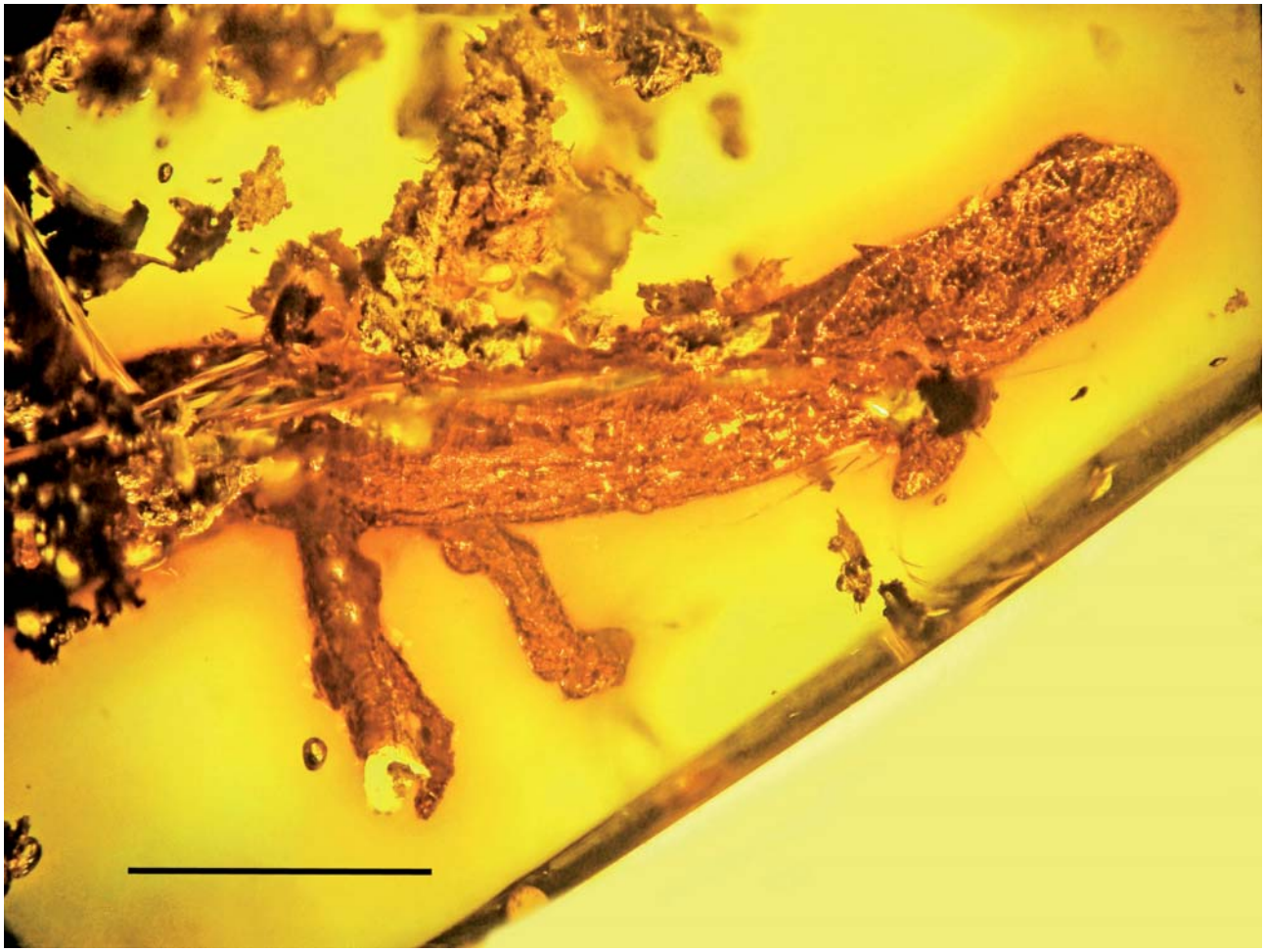


Fig. 2. Lateral view of right side of fore body of *Palaeoplethodon hispaniolae* gen. n., sp. n. in Dominican amber. Bar = 2.0 mm.

panied by a darkening of the tissues, the original color was probably somewhat lighter.

Based on its small size and apparent slight ossification of the skeletal elements, the fossil is considered to be a hatchling. One area that showed some faint ossification with x-rays was the region of the maxilla (Fig. 11). Additional evidence of bone structure was observed with the light microscope. An exposed portion of the right forelimb showed portions of the radius and ulna (Fig. 6, arrow) and phalanges were evident on ventral surface of the right forefoot (Fig. 7, arrow). Elements along the spine (possibly the notochord) represented initial stages of vertebral formation (Fig. 12). Further evidence of bone presence was the stub of the humerus protruding from the severed left forelimb (Fig. 13, arrow).

The diminutive size of the fossil (total length of 19 mm and snout-vent length of 9.0 mm) is similar to the dimensions of some extant tropical plethodontid hatchlings. Hatchlings of *Nototriton picadoi* (Stejneger, 1911) averaged 12.2 mm in total length and 7.8 mm in snout-vent length (Bruce 1998). Hatchlings of *Bolitoglossa subpalmata* had a snout-vent length from 9.2-11.0 mm (Vail 1968) while hatchlings of *B. diminuta* measured 8.0 mm or less from snout to vent (Robinson 1976) (Fig. 4B).

4. Discussion

All extant salamanders in the New World tropics belong to the family Plethodontidae (Wake 1987; Wake & Lynch 1976). One of the most successful genera in this family is *Bolitoglossa* Peters, 1863, with numerous arboreal and terrestrial species ranging from Mexico through Central America and into South America (Wake & Lynch 1976). This genus is the most widespread of all tropical genera and contains about 20% of all currently recognized species of salamanders (30% of plethodontids)(Wake 1987). Some characters of the fossil, such as an apparent number of 13-14 costal grooves, absence of a discernable sublingual fold and webbed feet and hands with 5 digits in the foot, align it with the genus *Bolitoglossa* (Wake 2012). If the fossil was an ancient lineage of *Bolitoglossa* (Fig. 14), based on its large, webbed hands and feet, it would fall into the old “alpha” section (Wake & Lynch 1976). The species of this section are now sorted into several

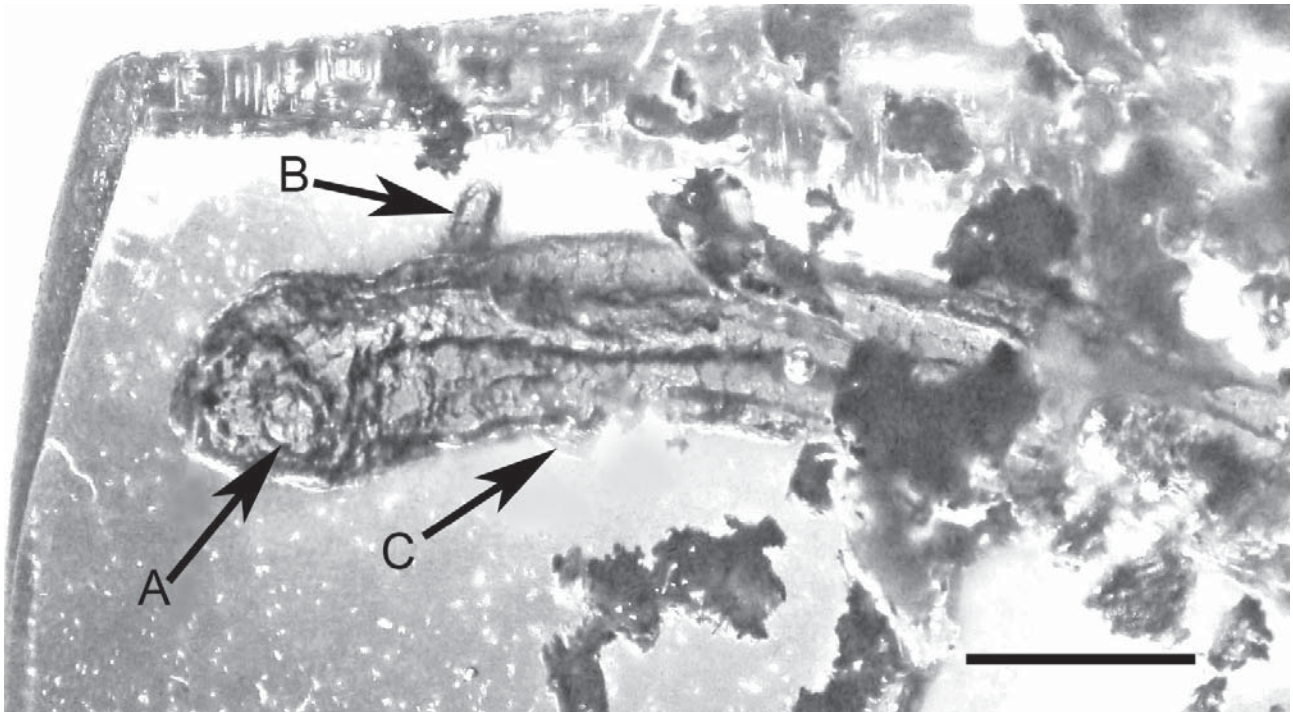


Fig. 3. Dorsal-lateral view of left side of fore body *Palaeoplethodon hispaniolae* gen. n., sp. n. in Dominican amber. A = eye, B = right leg, C = remains of left leg. Bar = 1.5 mm.

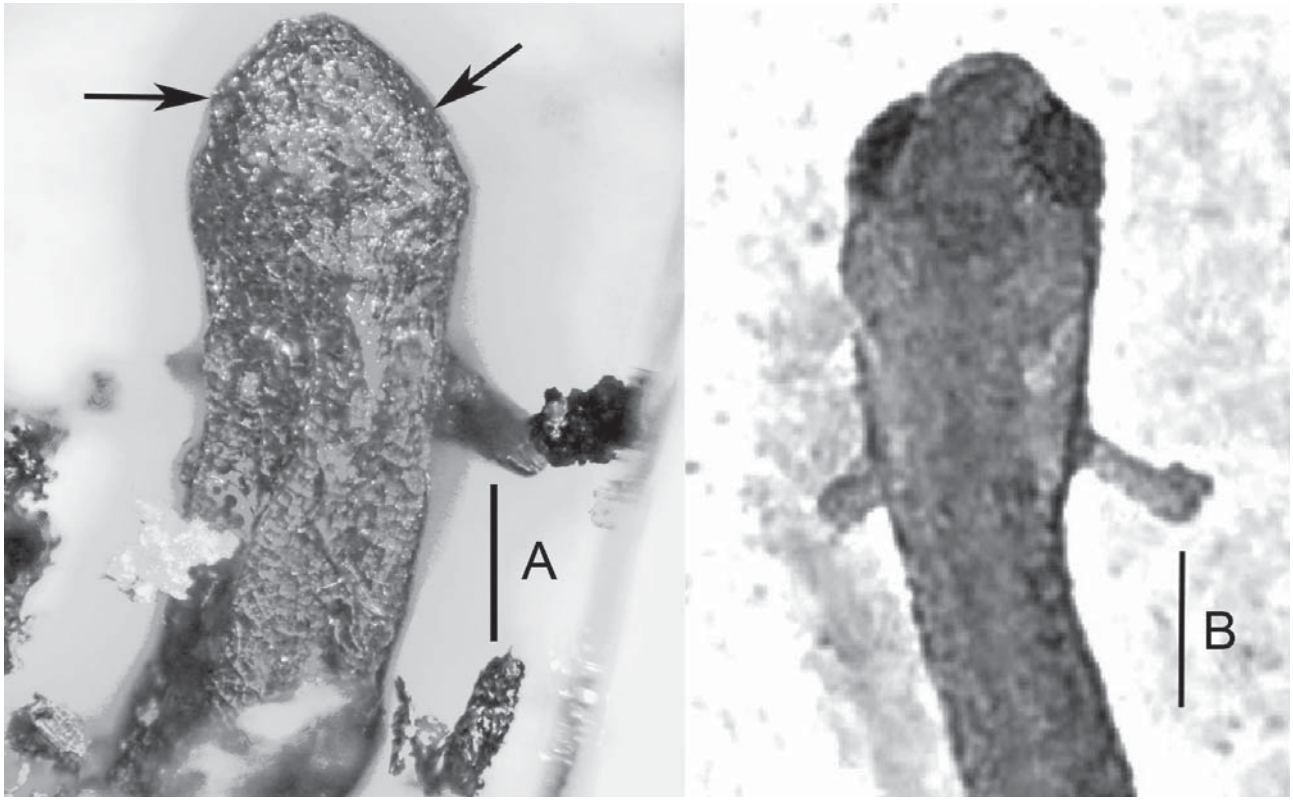


Fig. 4. A. Dorsal view of fore body of *Palaeoplethodon hispaniolae* gen. n., sp. n. in Dominican amber. Scale bar = 0.70 mm. B. Dorsal view of fore body of a hatchling *Bolitoglossa diminuta* Robinson from Costa Rica. Bar = 1.0 mm.

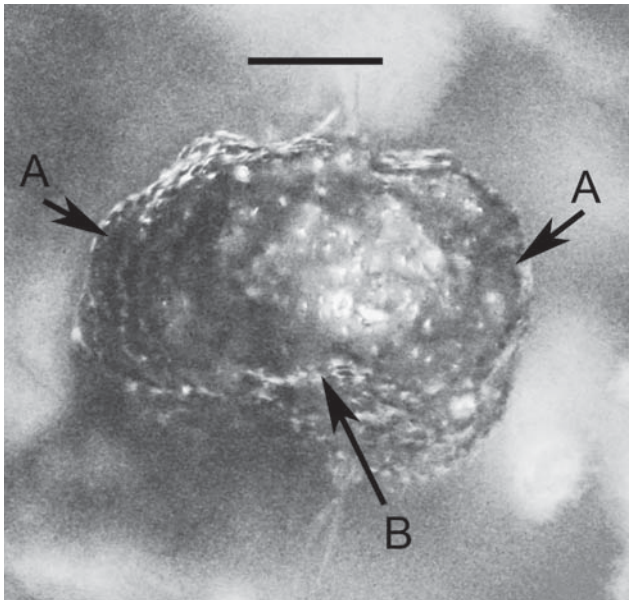
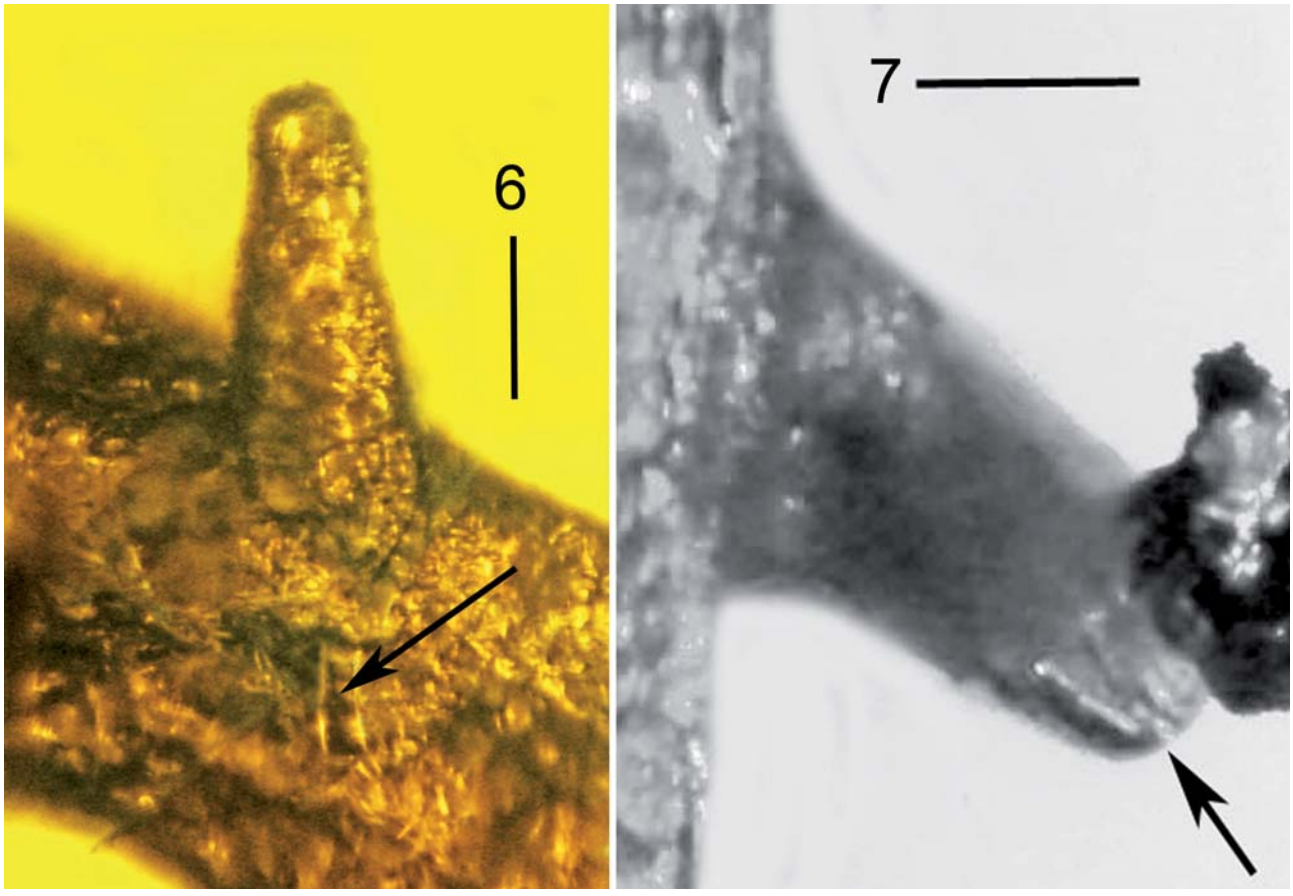


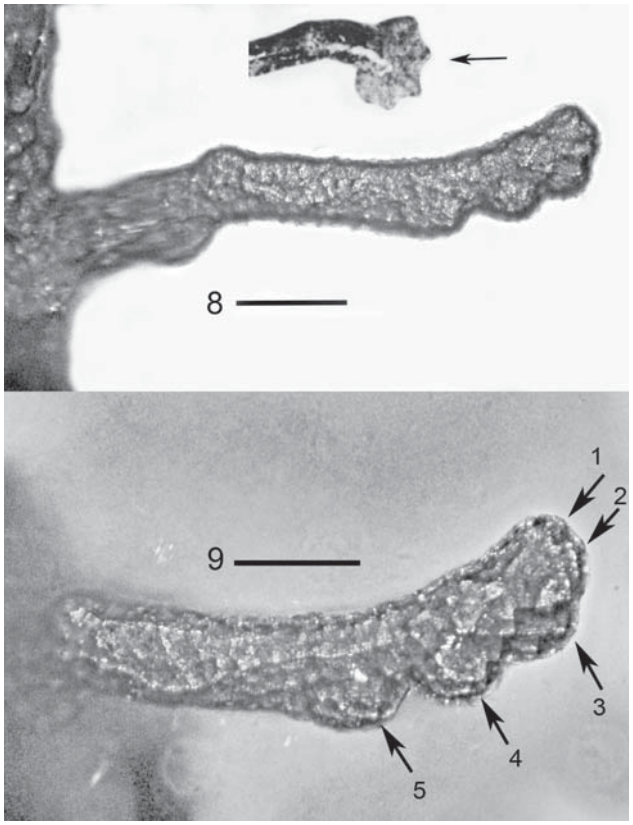
Fig. 5. Frontal view of head of *Palaeoplethodon hispaniolae* gen. n., sp. n. in Dominican amber. A = eyes, B = mouth. Bar = 0.50 mm.

subgenera, including miniaturized species of *Nanotriton* and *Mayamandra* in Mexico and northern Central America, and *Bolitoglossa*, which ranges from northeastern Mexico to Bolivia and western Panama (WAKE & LYNCH 1976). In a provisional phyletic tree of the Plethodontidae, *Palaeoplethodon* is shown as an early offshoot of the tribe Bolitoglossini (Fig. 15).

The shape of the feet is curious, especially the rounded foot on the right forelimb that lacks any evidence of toes. The presence of phalangeial bones at the periphery (Fig. 7) shows that the toes are present. There are various degrees of toe fusion in salamanders, however there is usually some indication of individual digits even if they are reduced to two or three small projections (Fig. 8, insert). Whether this condition represents feet that are incompletely developed (pedomorphic) is unknown (WAKE 1987). The shape of the hind foot is unusual in another respect: it is longer than wide, yet fully webbed, a condition not known in living salamanders. Even if the basal swelling is the ankle, then the remaining portion is still longer than wide (Fig. 9). With *Bolitoglossa insularis*, where there is complete webbing of the digits, the manus is still evident and the



Figs. 6–7. *Palaeoplethodona hispaniolae* gen. n., sp. n. in Dominican amber. **6**.Ventral view of reflexed right forelimb. Arrow shows region with exposed portion of humerus. Bar = 0.38 mm. **7**. Dorsal view of tip of right forelimb showing phalanges (arrow). Bar = 0.25 mm.



Figs. 8 –9. *Palaeoplethodona hispaniolae* gen. n., sp. n. in Dominican amber. **8**. Right hind limb. Insert (arrow) shows webbed foot of the extant *Bolitoglossa mexicana*. Bar = 0.60 mm. **9**. Right hind limb. Numbers indicate likely position of webbed toes. Bar = 0.45 mm.

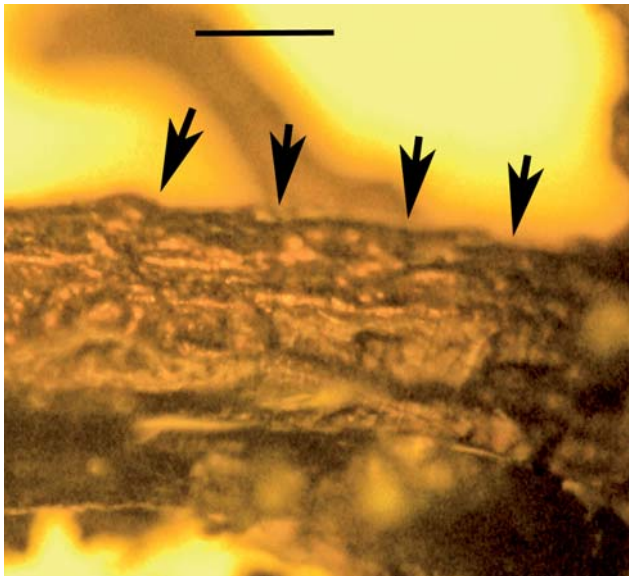


Fig. 10. Trunk portion of *Palaeoplethodon hispaniolae* gen. n., sp. n. in Dominican amber showing four faint costal grooves (arrows). Bar = 0.6 mm.

foot pad is wider than the wrist (carpels) (Sunyer et al. 2008). These modified digits are depicted in a reconstruction of the fossil as it could have existed in the Dominican amber forest (Fig.16).

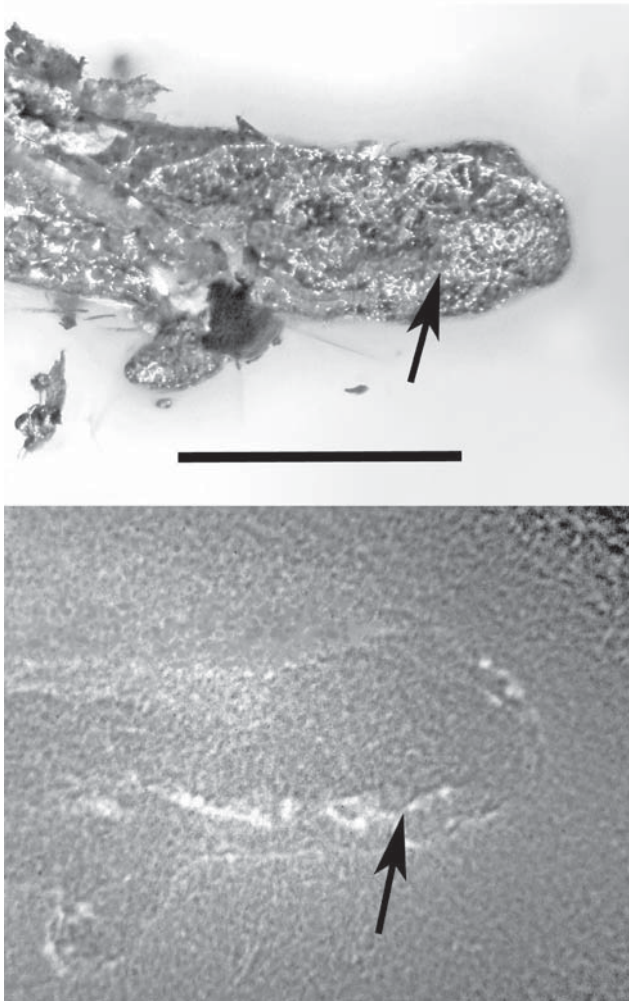
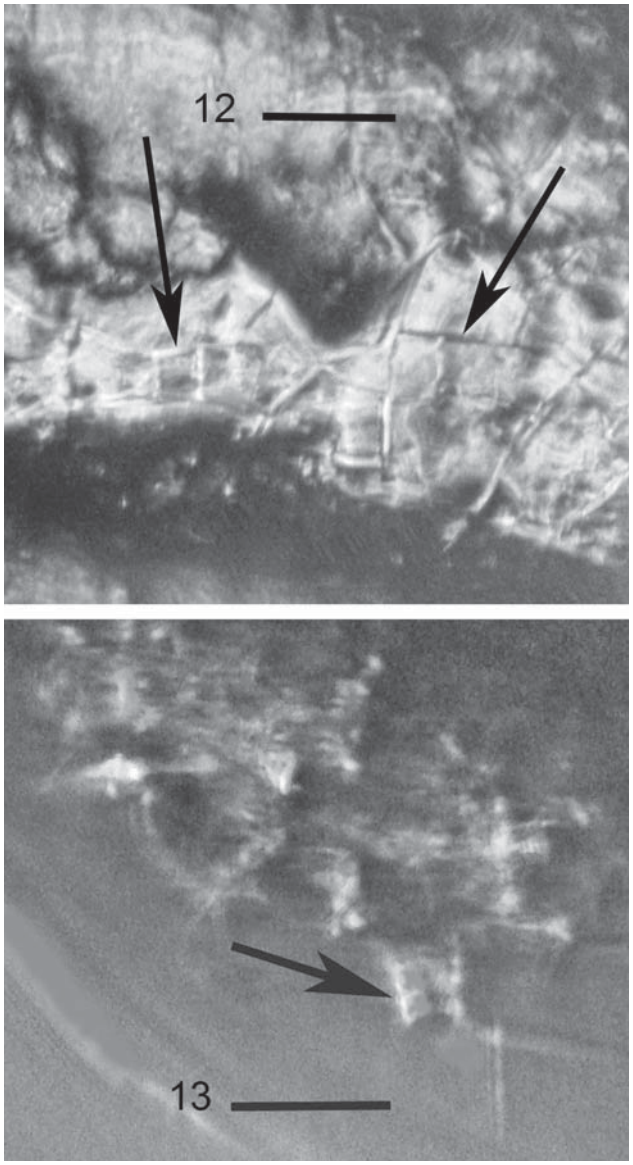


Fig. 11. Upper figure shows lateral view of head region of *Palaeoplethodon hispaniolae* gen. n., sp. n. in Dominican amber. Lower figure is an X-ray of the same region shown in the upper photo. Arrows in both photos point to the region of the maxilla. Bar = 50 µm.

No undisputed records of salamanders are known from the West Indies or from the entire Caribbean region today (Williams 1999). In 1879, Peters described the salamander *Spelerpes infuscatus*, supposedly from Haiti. However, the collection data were questionable and Dunn (1926) regarded the specimen as *Lineatriton lineolus* (Cope) from Mexico. Later, Wake (1993) studied the holotype of *S. infuscatus* in the Hamburg Museum and noted that it has a subocular groove that intercepts the lip, an



Figs. 12–13. *Palaeoplethodona hispaniolae* gen. n., sp. n. in Dominican amber. **12**. Spinal element (arrows) in lumbar region. Bar = 0.1 mm. **13**. Portion of humerus (arrow) protruding from the severed left front leg. Bar = 0.1 mm.

autapomorphy of the Mexican genus *Thorius*, which has nostrils of similar size and shape. WAKE (1993) considered *S. infuscatus* as a possible synonym of *Thorius narisovalis* TAYLOR from Oaxaca. No salamanders have been collected since from the West Indies (WILLIAMS 1999).

It is possible that *P. hispaniolae* reached its present location in the Dominican Republic by a vicariance event. The ancestors of *P. hispaniolae* could have migrated from North America onto the Proto-Greater Antilles archipelago when it was in contact with North and South America in the Late Cretaceous or Paleogene (ROSEN 1975). When the Proto-Greater Antilles separated from North and South America and moved eastward into the Caribbean, it carried a menagerie of animal and plants from both continents. Portions of this land mass, including higher elevations of the Dominican Republic, remained emergent during this period (LEWIS ET AL. 1990, ROSS & SCOTESE 1988, DONNELLY 1988). Other possible scenarios of how *P. hispaniolae* arrived in its present location are overwater dispersal on drifting flotage. This scenario was considered a likely means of dispersal for eleutherodactyline frogs HEINICKE et al. (2007) from South America to the Caribbean in the early Cenozoic. However, this amphibious lineage, which is represented by numerous species of *Eleutherodactylus* DUMÉRIL & BIBRON in South America as well as by fossils in Dominican amber, also could have arrived in Hispaniola by vicariance (POINAR & CANNATELLA 1987; WILLIAMS 1999).

Extinction of the *Palaeoplethodon* lineage could have been due to climatic deterioration. Periods of cooling and/or drying from the Eocene to Miocene were associated with numerous extinction events in the Americas. A significant cooling period that occurred during the Middle to Late Eocene (~37-38 mya) was followed by a cooling and drying period at the transition of the Eocene and Oligocene (~33 mya) and a cooling period during the Oligocene-Miocene transition (~20-23 mya) (PROTHERO 1994).

Previous fossil plethodontids are represented by tracks or skeletal parts (HOLMAN 2006). These include isolated vertebrae from the Mio-Pliocene of northeastern Tennessee (BOARDMAN & SCHUBERT 2011), tracks and vertebrae of a Mio-Pliocene *Batrachoseps* from California (CLARK 1985; HOLMAN 2006), an otic bone of a Mio-Pliocene *Aneides lugubris* (CLARK 1985), a "*Plethodon*-like" trunk vertebra from a Mio-Pliocene site in Texas (PARMLEY 1989), indeterminate plethodontid material from a Late Tertiary site in Indiana (FARLOW et al. 2001), vertebrae from a

Fig. 14. The extant *Bolitoglossa chinanteca* from Oaxaca, Mexico. Note the webbed feet, which are characteristic of many members of the tribe Bolitoglossini. (Photograph by SEAN ROVITO).

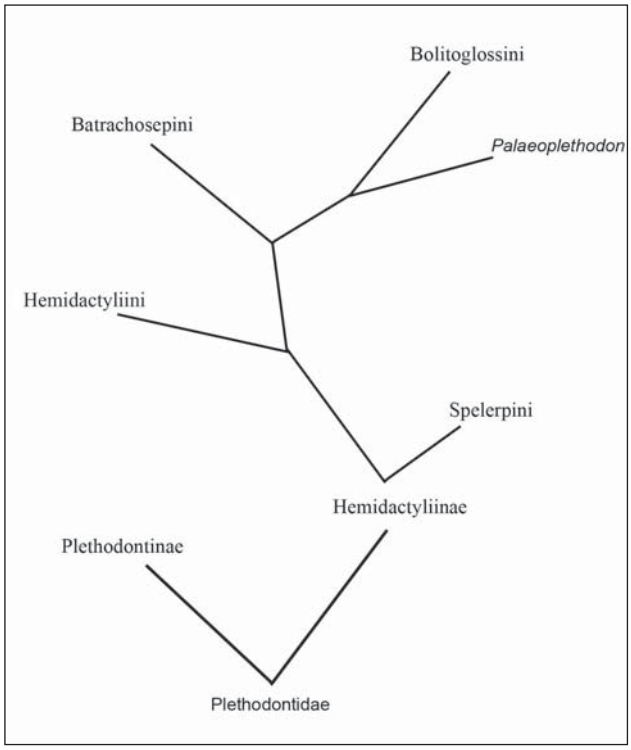


Fig. 15. Provisional phyletic tree of the family Plethodontidae showing *Palaeoplethodon* as an early offshoot of the tribe Bolitoglossini.

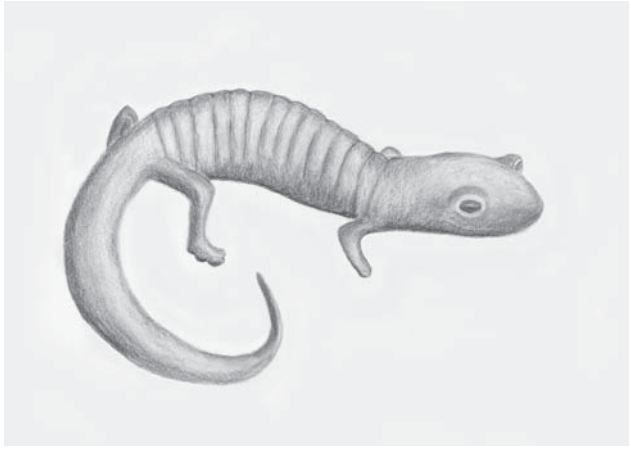


Fig. 16. Reconstruction of *Palaeoplethodon hispaniolae* gen. n., sp. n. as it could have appeared in the Dominican amber forest (GP).

Lower Miocene location in Montana (Tihen & Wake 1981) and remains of *Plethodon* and *Aneides* from the Arikareean Late Oligocene (approximately 26-28 mya) of Montana (Rasmussen & Prothero 2003). The present fossil is the most complete fossil plethodontid, the first fossil salamander from the American tropics and the only undisputed salamander from the Caribbean.

The presence of *P. hispaniolae* gen. n., sp. n. in amber appears to have been the result of a fortuitous but traumatic event when the salamander was attacked by a predator, probably soon after it hatched. During the struggle, the salamander's left forelimb was severed and in an effort to escape, the amphibian fell into a resin deposit. Based on its relatively long hind legs and strongly webbed hands and feet, *P. hispaniolae* was likely an arboreal species (Wake & Lynch 1976) that was associated with bromeliads, as with other Neotropical plethodontids (Stejneger 1911; Picado 1913; Wake 1987; Ruano-Fajardo et al. 2014). The bromeliad habitat is known to harbor a number of predators that could have attacked such a small salamander (Calvert & Calvert 1917; Picado 1913).

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